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Survey of Biomass and Net Production of Higher Plant Communities in Fishponds

Based on a paper presented at the symposium on "Biological Productivity of Freshwater Plant Communities" at the XIIth International Botanical Congress in Leningrad, July 5, 1975.

Keywords

Biomass, Net primary production, Plant communities, Aquatic and marsh higher plants (macrophytes), Plant life-forms, Fishpond management, Czechoslovakia

Abstract

After a brief account of both past and present fishpond management and of its impact on the fishpond vegetation of higher plants, a survey is given of the biomass and total net production in various types of communities constituting this vegetation. Relatively stable and unstable communities are distinguished and further differentiated by the dominant plant life-forms. The biomass and production data are highly variable, depending on actual conditions in the fishpond habitats, but the maximum recorded values of annual net production (in terms of dry matter produced per year) appear to decrease in the following order: the communities dominated by ochthohydrophytes (over $3 \text{ kg} \cdot \text{m}^{-2}$)—hydroochthophytes and euochthophytes (about $2 \text{ kg} \cdot \text{m}^{-2}$)—pleustophytes and aerohydatophytes (upto $1 \text{ kg} \cdot \text{m}^{-2}$) euhydatophytes (upto $0.5 \text{ kg} \cdot \text{m}^{-2}$). The original data were gathered in Czechoslovakia and the conclusions apply to fishponds in Central Europe.

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Lakes, standing waters in river alluvia, marshes and swamps, all these are naturally flooded or wet areas that have arisen through long-term geomorphological and hydrological processes. Their plant-species populations have passed through a long history of adaptation to their habitats. This paper deals, however, with the vegetation of man-made fishponds, taking those in Central Europe as an example.

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FISHPOND HABITATS

The fishponds are artificial reservoirs greatly varying in size, most of them constructed some 4 to 6 centuries ago, mostly on wetland sites. Their surface area varies from a few hundred square meters to several square kilometers but their depth varies less: only rarely do the average and maximum depths exceed 1.5 and 4 m, respectively.

The higher-plant communities of the fishponds are derived from those of the original wetlands and shallow waters. Some differences have, however, come into being, and their character and extent have been changing along with the ways of managing the fishponds. Four principal management categories of fishponds may be distinguished:

(a) Fry and fingerling ponds, small (mostly about 0.01 km^2 or less) and shallow (< 1 m), usually more or less densely vegetated, filled and drained each year. The reed belt is usually negligible.

(b) Hibernation ponds, of medium size (mostly 0.05 to 0.4 km^2); relatively deep and/or with appreciable exchange of water in winter when they are kept at a high watermark and stocked with fish. These ponds are frequently colonized by both submerged and floating vegetation; the reed belt is usually narrow as its width is controlled by cutting.

(c) Main fish-producing ponds, medium-sized to large (some 0.25 to 5 km^2). A two-year rotation prevails nowadays: a pond is stocked in spring of one year to be drained and cropped in autumn of the subsequent year. Dense submerged or floating vegetation only rarely develops in these ponds; the reed belt tends to grow wide unless radical control measures are applied.

(d) Special ponds whose main purpose is other than fish-farming: recreation, water storage sewage disposal or treatment, etc.

Most fishponds are managed as the main fish-producing ponds (category c) for most of the time (the same pond may serve different purposes in different years). The principal fish species cultivated is carp (*Cyprinus carpio* L.). While fish production has always been the main objective, the management of the main ponds has passed through three characteristic stages during its history:

(a) Extensive fish-farming, mostly relying on the natural food chains supporting the fish-Their growth was slow; consequently, the rotation period was long: 5 to 10 years. After each rotation period, the pond was kept summer-drained, i.e., left empty for one season, with field crops cultivated in the fertile bottom mud. This extensive management was gradually abandoned during the 19th century.

(b) Moderately intense fish-farming in which the primary production is enhanced by fertilizing or manuring the water, and the fish receive some additional food. The rotation period is mostly shortened to 3 to 5 years, and summer-drainage is less regular. Instead, the ponds are frequently winter-drained, i.e., left empty after the autumnal drawdown. The shores may then remain emerged during the first year of the rotation; this partly compensates for the lack od summer-drainage. The growth and spreading of the reed belt can no longer be checked by frequently ploughing up the pond shores. Cutting—in summer—thus becomes the most important control practice preventing undesirable development of the higher plants in general. The moderately intense management prevailed for about a century, from 1860 to 1960. During that time, the fish yields rose from some 80 kg to 250 kg live mass per hectare.

(c) Highly intense fish-farming of the present time. High doses of fertilizers are applied to the fishpond water either directly (by the fishpond managers themselves) or indirectly and unintentionally (coming in with agricultural wash-out or with drainage water from surrounding arable land). The fish are fed regularly, richly and in a sophisticated way (special fodder mixtures, etc.). The rotation period is shortened to 2 years (sometimes only 1 year). Fish-farming is frequently combined with duck-farming in the same ponds. Summer-drainage has been practically abandoned but winter-drainage still persists, and so, often, does the partial filling of the ponds for the first season of the rotation period. The aquatic vegetation develops poorly or not at all whereas the reed belt can profit from the increased mineral nutrient contents both in the water and the mud. A reduction of open water area is prevented by periodically scraping off the whole reed belt with bulldozers; the removed material is piled up along the shores. Cutting serves as an additional measure for controlling both the aquatic and the shore vegetation. This system of intense fish-farming has developed during the last 20 years. It has not only resulted in a significant increase in fish yields (upto 400 to 700 kg per hectare) but also in a pronounced deterioration of water quality in the fishponds. Most of the submerged and floating plant species are affected adversely, and only a few tolerant species sometimes take advantage of the heavily eutrophicated conditions (e.g., *Spirodela polyrhiza*, *Lemna* spp., *Potamogeton pectinatus*).

This brief history accentuates two important circumstances:

(a) Despite many similarities, the fishpond vegetation can never be quite the same as that of natural waters or wetlands.

(b) The fishpond vegetation (and, indeed, the complete biotic community in a fishpond) represents a set of successional stages in a hydrosere whose progression is held back by permanent energy input associated with the fishpond management.

The age of a fishpond is of importance: the plant communities tend to be richer and more complex in an older pond; in a young one, they are usually simpler and species-poorer: ecologically plastic species populations become expansive. Most fishponds also represent far more open ecosystems than natural lakes: the degree of openness to migrating plant propagules depends mainly on water supply to a pond. Most open, in this respect, and hosting phytocenoses of a relatively rich species composition are those ponds which are fed with water from a river or creek. Here, it is also relatively easy to keep the water level at a fixed watermark. The structure of the phytocenoses then varies but little with time. The "sky-fed" ponds, with water supplied by local rainfall, represent the opposite; systems relatively closed to new propagules but hosting rather varied phytocenoses because of the wide fluctuations of water level. The sets of species forming these phytocenoses are, however, more restricted here than in the former case.

The actual position of water level at any one site in a fishpond determines the ecophase. Four principal ecophases may be distinguished, as shown in Fig. 1: hydrophase and the littoral, limosal and terrestrial phases. Individual plant life-forms vary in their adaptability to each ecophase. The sequence of ecophases during one year is called an ecoperiod. A sequence of ecoperiods from one long-term (one season's or longer) drawdown or reatreat of shoreline to another, may be called an ecocycle. The fishpond vegetation is usually most variable at the onset of an ecocycle: a characteristic sequence of ecoperiods during the first four years of an ecocycle is presented in Table 1. For details of the principles of rhythmic changes in freshwater littoral and aquatic vegetation, brought about by water-level fluctuations, see HEJNÝ (1957, 1960, 1971, 1978), HEJNÝ et HUSÁK (1978) and HEJNÝ et KVĚT (1978).

Both the rhythm and extent of the water-level fluctuations determine the balance between the accumulation of organic matter in a pond, and its decomposition and mineralization. In long-term run, accumulation prevails in fishponds; hence the importance of periods of low water level or summer-drainage during which mineralization is enhanced. The accumulation of autochthonous material usually combines with sedimentation of allochthonous material brought in with inflowing water, and with shore erosion and bottom deposition of the eroded material. The net outcome of all these processes is a gradual filling up of a fishpond with mud and silt; this is accompanied by a succession leading from aquatic to terrestrial communities and giving rise to their distinct zonation. To slow down or temporarily to revert this trend is one of the principal aims of fishpond management. Yet, diverse habitats co-exist in fishponds. The scheme given in Fig. 2 illustrates the distribution of substrates in an idealized fishpond. In real situations, different plant communities develop on different sites along fishpond shores in dependence on the local long-term balance between sedimentation and accumulation on the one hand, and erosion and organic-matter decomposition on the other. The morphometry of each fishpond acts as one of the factors governing the spatial distribution of these processes.

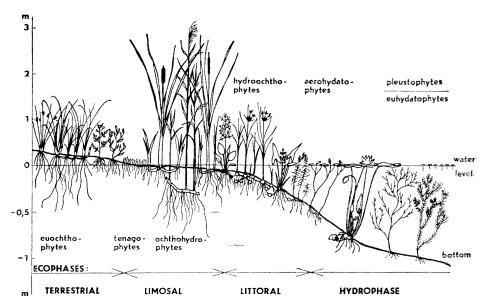


Fig. 1. Idealized transect across the shore of a pond filled to normal watermark, presenting typically developed ecophases and representatives of the plant life-forms typical of each ecophase. (Drawing by ZDENKA HROUDOVÁ).

Table 1. Four principal possible types of ecoperiods and their effects on the stabilized (A) and	ł
unstable (B) higher-plant communities occupying the fishpond sublittoral ¹ and eulittoral ¹	

Ecoperiod	Changes in the vegetation
1. Limoso-terrestrial: water level falling, shoreline retreating	 A: Degradation of the reed-belt and of the tall sedge communities B: Onset, full development and disappearance of stenoecious ephemeral communities of emerged bottoms; alliances: Bidention – Nannocyperion – Littorellion – Agropyro – Rumicion crispi
2. Limoso-littoral: water level rising, shoreline advancing.	A: Gradual regeneration of the reed-belt communities, their slow advance into the sublittoral.B: Onset of the stenoecious and ephemeral communities in the littoral
3. Littoral-hydric: both water level and shoreline returning to their usual positions	A: Gradual stabilization of phytocenoses in the whole fishpond.B: Full development to disappearance of stenoecious communities in the littoral
4. Constant hydrophase: water level without substantial change	A: Stabilization of the fishpond phytocenosesB: Disappearance of stenoecious communities in the fishpond

¹ Although the terms epilittoral, eulittoral and sublittoral and even pelagial are often applied to fishponds, they describe situations only roughly analogous to those in lakes. In fishponds, there is, in fact, no pelagial zone that would be too deep for the higher-plant vegetation to develop.

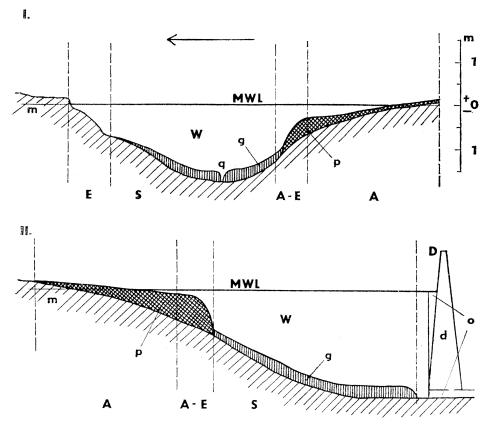


Fig. 2. Distribution of substrates in various pond zones: I. Transversal section across an idealized pond, the arrow indicating the prevalent wind direction. II. Longitudinal section along an idealized pond. Abbreviations and symbols: A - accumulation zone; A-E - accumulation-and-erosion zone; D - dam; E - erosion zone; MWL - mean water level; S - sedimentary zone; W - water; d - dam body; g - gyttja; m - mineral subsoil or bedrock; o - outlet; p - peat accumulated (autochthonous organogenic material); q - drainage ditch. (Drawing by ZDENKA HROUDOVÁ).

FISHPOND VEGETATION

The vegetation of any fishpond usually comprises a number of plant communities which, in turn, contain species differing in both life and growth form. Various classifications of the life and growth forms of aquatic and wetland higher plants have been proposed. The life-form system of HEJNÝ (1960) has been combined with DEN HARTOG'S and SEGAL'S (DEN HARTOG et SEGAL 1964) system by HEJNÝ (1971). The latest version of this combined system, worked out by HEJNÝ et SEGAL (in press) is used in this paper. The plant communities colonizing the fishponds may also be classified phytocenologically, as in HOLUB et al. (1967) and HEJNÝ et HUSÁK (1978). For a schematic presentation of the life forms in their typical habitats see Fig. 1. Complete plant communities comprising a single life form are rather rare, a classical example being duckweed communities of *Lemna* and *Spirodela* in village ponds. Mostly, it is only synusia that comprise only one life form, e.g., a pleustophyte synusium of *Lemna* and *Riccia* in a community of dominant *Typha angustifolia*, an ochthohydrophyte.

An assessment of the role played by various plant-community types in fishpond ecosystems must be based on their functional characteristics. A great step forward was made during the International Biological Programme (IBP) in 1965-74, when interest was focussed on the reed-belt communities dominated by ochthohydrophytes such as *Phragmites*, *Typha* or *Schoenoplectus* (phytocenological alliance *Phragmition communis* W. KOCH 1926). Now, the interest has been widened to communities dominated by other life forms occurring both waterwards and landwards from the reed belt.

DATA ON BIOMASS AND PRODUCTION

A brief account now follows of the biomass and ne_{ν} production of the fishpond vegetation. We may recognize two kinds of communities distinguished by their reactions to water-level fluctuations:

A. Stabilized communities belonging, more or less, to the classical "landbuilding" succession seres leading from aquatic to terrestrial communities. The succession is favoured by a rather stable water level resulting in a fixed spatial pattern of ecophases.

B. Unstable communities whose existence depends on water-level fluctuations. Different community types will attain their optimum development at different stages of these fluctuations.

This survey of biomass and production—all data in terms of dry mass per 1 m^2 —is based on a wealth of data published in HEJNÝ (1960), in a number of papers contained in the reports edited by DYKYJOVÁ (1970), HEJNÝ (1973) and KVĚT (1973) as well as in the papers and theses by DYKYJOVÁ (1971a, b), DYKYJOVÁ et al. (1970, 1971, 1972), DYKYJOVÁ et ONDOK (1973), DYKYJOVÁ et HRADECKÁ (1973), FIALA (1976, 1978), FIALA et al. (1968), FIALA et KVĚT (1971), HUSÁK (1971), HUSÁK et HEJNÝ (1973), JAKKLOVÁ (1975), KVĚT (1971, 1975), KVĚT et al. (1969), ONDOK (1969, 1970), REJMÁNEK (1975), REJMÁNKOVÁ (1973, 1975, 1978, 1979), RYCHNOVSKÁ et al. (1972), ÚLEHLOVÁ (1976), VELÁSQUEZ (1975), and on unpublished data by I. FJØRTOFT (in litteris), S. HEJNÝ et K. GREGOR (in litteris) and Š. HUSÁK et J. KVĚT (in litteris). These authors also desribe the methods used. The principal results of the ecological investigations of fishpond littorals are summarized in DYKYJOVÁ et KVĚT (1978).

Data on biomass, net production and ash content (needed for estimating the net production of organic matter) are available on both the stabilized (A.) and unstable (B.) community types.

A. Stabilized communities

A.1. Communities dominated by euochthophytes

In fishpond littorals, these communities are represented by those of tall sedges (order *Magnocaricetalia* PIGNATTI 1953). They are dominated either by tussocky sedges such as *Carex elata*, or by sedges forming a more or less continuous cover such as Carex gracilis or C. riparia. The production ecology of sedge marshes has been rather little studied in general (see, e.g., BERNARD 1973) as well as on fishpond shores. Estimates by NEKVASILOVÁ (1973) for a Caricetum elatae (KERNER 1858) KOCH 1926 and data by several of the authors quoted above on Caricetum gracilis ALMQUIST 1929 communities, indicate that their seasonal peak aboveground biomass will vary, in both types, from about 0.4 to 1.7 kg. m⁻². A seasonal peak leaf area index of about 5 has been recorded in a Caricetum gracilis in South Bohemia (I. FJØRTOFT, in litteris). A Carex undergrowth is not uncommon in limosal reed-belt communities in fishponds, but these communities are dealt with under the next heading.

A.2. Communities dominated by ochthohydrophytes

This life form is representative of the "classical" helophytes forming the fishpond reed belts. These were studied particularly intensely. Most attention was paid to the invasion stages of the communities dominated by *Phragmites australis* (= *P. communis*), *Glyceria maxima*, *Typha angustifolia*, *T. latifolia*, *Schoenoplectus lacustris*, *Sparganium erectum* and *Acorus calamus*, all belonging to the alliance *Phragmition communis* W. KOCH 1926. For communities of the association *Equise-tetum fluviatilis* (NOWIŃSKI 1928) STEFFEN 1931, also belonging to that alliance, there exists a single estimate of peak aboveground biomass: 1.24 kg . m⁻² (S. HEJNÝ et K. GREGOR, in litt.) and one of belowground biomass: 0.88 kg . m⁻² (D. DYKYJOVÁ, in litt.). In fishponds, the most widespread dominants are the first three of the species listed above but *Sparganium erectum* and *Acorus calamus* (as well as *Typha latifolia* and *Glyceria maxima*) are likely to gain more ground with the advancing eutrophication of fishponds.

The highest recorded values of peak aboveground biomass vary from less than 1 kg \cdot m⁻² in an Acoretum calami EGGLER 1933 community to some 3.5 kg \cdot m⁻² recorded in small plots in Phragmitetum communis (GAMS 1927) SCHMALE 1939 or Typhetum angustifoliae (ALLORGE 1922) Soó 1927 communities in eutrophic habitats at littoral ecophase. Even here, however, the average biomass over larger areas is usually less than 2 kg \cdot m⁻². The shoots of the tallest plants are as high as 3.5 to 4 m in such stands. Lower maximum values of peak aboveground biomass, not exceeding 2 kg \cdot m⁻², originate from stands at limosal ecophase, which often comprise a taller (upto 2.5 m) storey of Phragmites and an understorey (upto 1 m) of sedges such as Carex riparia or C. gracilis. At terrestrial ecophase or at a stage of degradation, the ochthohydrophyte-dominated communities attain a peak aboveground biomass of some 1 kg \cdot m⁻² or less.

The underground : aboveground biomass ratio (R/S ratio) has also been investigated. In mature invasion communities it may vary from some 0.4 to 0.6 in nearly pure stands of *Typha latifolia* to 3 to 4 in those of *Schoenoplectus lacustris* or *Phragmites*. Under conditions suppressing shoot development or in situations in which the rhizomes survive for many years, the R/S ratio may increase to 5 or even more (7.6 in a degenerating *Glycerietum maximae* HUECK 1931). The variable R/S ratio complicates the estimation of total biomass, not to speak of total annual net production in these communities. It seems to be the survival time of the rhizomes that determines the size of the permanent underground biomass pool and thus controls the value of total biomass recorded at any one time. The maximum values of total biomass found in ochthohydrophyte-dominated communities are therefore highly variable: from 1.7 kg \cdot m⁻² in an Acoretum calami EGGLER 1933 to 9.5 kg \cdot m⁻² in a well-developed pure Phragmitetum communis at littoral ecophase.

Even more difficult to obtain are reasonable estimates of total net annual production. The net aboveground production is mostly only somewhat higher than the seasonal peak aboveground biomass, exceeding it by 5 to 20% according to species and conditions for shoot development (an exception are, of course, heavily grazed or infested plots, see PELIKÁN et al. 1970, KVĚT et HUDEC 1971, SKUHRAVÝ 1978, and others). The net undergound production is mostly approximated as a fraction of rhizome biomass divided by the survival time of the rhizomes. Alternatively, the pattern of dry matter distribution between individual plant parts, found in 1 to 3 years old culture of the dominant species (see DYKYJOVÁ et VÉBER 1978 and FIALA 1978) is assumed to be valid for mature stands as well. The communities formed by the three principal dominants occupying the largest areas in fishponds, attain the highest maximum values of annual net production: Phragmitetum communis about $4 \text{ kg} \cdot \text{m}^{-2}$, Glycerietum maximae and Typhetum angustifoliae, both 3.4 kg. m⁻². In mature Typhetum angustifoliae communities, the total annual net production is less variable than in the other Phragmition communities: some 1.2 to 3.4 kg \cdot m⁻². This is evidently due to Typha angustifolia occupying a narrower range of habitats than the other dominant ochthohydrophytes do. The species cannot survive or withstand competition at a long-lasting terrestrial ecophase (HEJNÝ 1960).

The LAI values of the ochthohydrophyte-dominated communities characterize the size of their assimilatory apparatus. The radiation-intercepting and photosynthetic characteristics of their leaves and canopies will greatly vary (ONDOK 1977) and so will probably their total respiratory losses. For attaining much the same high production, a *Typhetum angustifoliae* develops an LAI of 4.4 or less while the *Phragmitetum communis* or *Glycerietum maximae* do an LAI between 5 and 9 to 10.

The ash content only rarely exceeds 10% in most ochthohydrophytes, only *Acorus calamus* and *Sparganium erectum* are usually richer in ash (11.5 to 14%). The energy content in ochthohydrophyte biomass therefore fluctuates about 17.6 kJ (= 4.2 kcal) per 1 g dry mass. (For more details see DYKYJOVÁ et PŘIBIL 1975.)

A.3. Communities of pleustophytes

The pleustophyte communities (of Lemna, Spirodela, Riccia, etc.) are structurally simple and their radiation-intercepting surfaces consist, as a rule, of a single layer of leaves or fronds. They tend to be most productive if they form a continuous carpet covering the water surface (LAI \doteq 1) and intercepting a great deal of the incoming radiation. Even a slight overlapping and mutual shading of the plants is known to have an adverse effect on the growth of Lemna (REJMÁNKOVÁ 1978, 1979). This fact sets an upper limit to the biomass of the pleustophyte communities: it hardly ever exceeds 0.25 kg. m⁻². But an easy vegetative spreading and rapid turnover of the biomass largely compensate for this drawback. Under favourable conditions of irradiance, temperature and mineral nutrient supply, for example in cultures, the doubling time of *Spirodela polyrhiza* and *Lemna gibba* may be as short as 3 to 4 days. In natural situations, a turnover factor of 1.5 to 2 applied to the biomass of highly productive stands of the *Lemnetum gibbae* MIYAWAKI et J. TÜXEN 1960 or *Lemno-Spirodeletum* KOCH 1954, yields estimates of their annual net production ranging between 0.3 and 0.4 kg. m⁻². Similar estimates have been made on the basis of seasonal changes in the relative growth rate.

A.4. Communities dominated by aerohydatophytes

Certain aerohydatophytes such as the nymphaeids (e.g., Nymphaea, Nuphar, Potamogeton natans) or trapids (Trapa natans) are favoured by a stable water level. They expand their leaves on the water surface and stretch them out into the air only if they become too crowded. In the nymphaeids, their long-lived and often bulky rhizomes, firmly rooted in the bottom, constitute most of the biomass; this is a factor seriously complicating any biomass and production estimates in these plants. Reliable data are therefore still lacking on stands of Nymphaea and Nuphar but some do exist on a Trapetum natantis TH. Müller et Görs 1960 and on a Nymphoidetum peltatae (Allorge 1922) TH. Müller et Görs 1960, from ponds: 0.11 and 0.18 kg. m⁻² as seasonal peak biomass. Higher values of about 0.2 kg. m⁻² have been ascertained in stands of nearly pure Potamogeton natans, which are derived from communities of the association Potamogetoneto natantis-Nymphaeetum candidae (HEJNÝ 1948) and sometimes thrive after their degradation through eutrophication.

A.5. Communities of euhydatophytes

In euhydatophyte communities, the photosynthetic production is limited by poor irradiance. Record biomass values and estimates of annual net production originate from a dense stand of *Elodea canadensis* in a eutrophic pond: 0.5 and 0.6 kg \cdot m⁻², respectively. The other high biomass values recorded in dense stands of euhydatophytes are lower, mostly between 0.3 kg \cdot m⁻² in a *Potamogetoneto* (*pectinati*)-*Zanichellietum pedicellatae* Soó 1947 and some 0.15 kg \cdot m⁻² in a *Potamogetonetum crispi* Soó 1927. Much less material is produced per unit area in loose stands or mere patches of euhydatophytes.

All biomass and production data in submerged aquatic plants are best expressed in terms of ash-free dry mass; their ash content usually varies between 15 and 30% of dry mass. The biomass and net production data quoted above therefore require appropriate corrections when evaluating the production of organic matter in the euhydatophyte and partly also aerohydatophyte and pleustophyte communities.

	nunity type(s) (ecophase)	Date(s) ³	Locality	
+ doi	minant species		pond name	region
l. l .1	Communities dominated by en Caricetum gracilis (terr.) C. gracilis, Calamagrostis canescens	uochthophytes (4 July 8 1976	A.1) Rožmberk Mokré louky	SB
.2	Caricetum gracilis (terr.) C. gracilis	July 1972	Opatovický	SB
.3	Caricetum gracilis (terrlim.) C. gracilis	July 1972	Opatovický	SB
.4	Caricetum ripariae (lim.) C. riparia	June 28 1971	\mathbf{Nesyt}	SM
.5	Phragmitetum communis (terr.) degrad. phase, Mentha aquatica Caricetum otrubae (terr.)	Aug. 28 1971 June 8	Nesyt	SM SM
.6×	C. otrubae, Potentilla anserina	1971	\mathbf{Nesyt}	SM
1.7×	Cuscuto-convolvuletum pulicarie- tosum-dysentericae (terr.) Pulicaria dysenterica	Aug. 28 1971	Nesyt	SM
2. 1 ×	Communities dominated by o Phalaridetum arundinaceae (terr.) P. arundinacea	chthohydrophyte June 28 1971	es (A.2) Nesyt	SM
2.2	Schoenoplectetum lacustris (lit.) S. lacustris	Aug. 25 1964	Starý Hospodář	SB
2.3	Typhetum latifoliae (lim.) T. latifolia	July 17 1963	Březovec	SB
2.4	Typhetum angustifoliae (lit.) T. angustifolia	July 17 1963	Březovec	SB
.5	Typhetum angustifoliae (lit.) T. angustifolia	July 25 1972	Opatovický	SB
.6	Glycerietum maximae (limlit.) G. maxima	July 5—30 1972	Opatovický	SB
.7	Glycerietum maximae (limlit.) G. maxima	July 1972	Opatovický	SB
.8	Glycerietum maximae (terr.) G. maxima	June 28 1971	Nesyt	SM
.9	Sparganietum erecti (lit.) S. erectum	Oct. 1 1966	Velké Stavidlo	SB
.10	Acoretum calami (lit.) A. calamus	July 16 196 3	Fabrický	SB
.11	Acoretum calami (lit.) A. calamus	June 1 1966	Kaprový	\mathbf{SB}
.12	Phragmitetum communis (lit.) Ph. australis	August 1968	10 sites	SB
.13	Phragmitetum communis (lit.) Ph. australis	July 1968	7 sites	SM

Table 2. Examples of biomass data assessed by the harvest method in various plant communities Moravia (SM). Names of communities after either HEJNÝ et HUSÁK (1978) or HUSÁK et HEJNÝ

Biomass ² (kg . m ⁻²) aboveground underground	total	Sampling pattern ³	Author(s)
$\frac{0.64}{2.32}$	2.97	$\frac{5 \times 0.25 \text{ m}^2}{3 \times 0.0625 \text{ m}^2}$	Novák (1977)
0.48	_	$3 \times 0.0025 \text{ m}^2$ $2 \times 1 \text{ m}^2 + 20 \times 0.25 \text{ m}^2$	Květ et Ondok (1973)
0.31 - 0.65 1.21	_	$4 \times 0.25 \text{ m}^2$	Květ et Ondok (1973)
1.01	-	4 ×1 m ²	Husák et Hejný (1973)
0.71	<u></u>	$4 \times 0.25 \text{ m}^2$	Husák et Hejný (1973)
0.51-1.01 0.54	<u> </u>	4 ×1 m ²	Husák et Hejný (1973)
$0.21 - 0.94 \\ 0.99 \\ \hline 0.66 - 1.27$	_	4×0.25 m ²	Husák et Hejný (1973)
1.27	_	4 ×0 .25 m²	Husák et Hejný (1973)
$ \begin{array}{r} \hline 0.78 - 1.57 \\ 1.93 \\ 1.71 - 2.03 \\ \overline{5.73} \\ \end{array} $	7.66	4 clusters of known area	FIALA et al. (1968)
4.88-6.18 1.29		$3 \times 1 \text{ m}^2$	S. Hejný et K. Gregor
$\overline{1.06 - 1.64}$ 1.37		$7 \times 1 \text{ m}^2$	(in litt.) S. Hejný et K. Gregor
$\overline{1.13 - 1.66}$ 1.78		1 transect of 0.25 m^2 plots	(in litt.) Ondok (1973)
0.69-1.21	-	0.25 m ² plots 3 transects of 0.25 m ² plots	Ondok (1973)
1.02	-	$4 \times 0.25 \text{ m}^2$	KVĚT et ONDOK (1973)
$\frac{0.99}{0.86 - 1.06}$		$4 \times 1 \text{ m}^2$	Husák et Hejný (1973)
$\frac{1.37}{1.30}$	2.67	8×0.5 m²	Dykyjová et Ondok (1973)
0.79	(cca 12%) —	$6 \times 1 \text{ m}^2$	S. HEJNÝ et K. GREGOR
$0.56 - 1.03 \\ 0.43 \\ \overline{1.18}$	1.61 (cca 12%)	$4 \times 0.5 \text{ m}^2$	(in litt.) FIALA et al. (1968)
$\frac{1.18}{0.82 - 1.48}$		$40 \times 1 \text{ m}^2$	Kvěr (1973b)
$\frac{0.82 - 1.48}{1.25}$ $\frac{1.06 - 1.51}{1.06 - 1.51}$	-	$28 \times 1 \text{ m}^2$	Květ (1973b)

occurring in fishponds in two regions of Czechoslovakia: South Bohemia (SB) and South (1973); the latter ones are marked by ${\bf x}$

	nunity type(s) (ecophase)	Date(s) ³	Locality	
+ do	minant species		pond name	region
.14	Phragmitetum communis (lit.) Ph. australis	$\frac{\begin{pmatrix} 6 \text{ successive} \\ \text{seasonal peaks} \end{pmatrix}}{\text{Oct. 11, 1969}}$	Opatovický site V	SB
.15	Phragmitetum communis (lim.) Ph. australis	$\begin{pmatrix} 6 \text{ successive} \\ \text{seasonal peaks} \end{pmatrix}$	Opatovický site S	SB
.16	Phragmitetum communis (lit.) Ph. australis	Oct. 14, 1969 July 15, 22 1966	Nesyt site T	SM
.17	Phragmitetum communis (lit.) Ph. australis	Nov. 11 1968	Rožmberk	SB
	Communities of pleustophytes			
.1	Lemnetum gibbae (lit., hydr.) L. gibba	June 1971–July 1972	Nesyt	SM
.2	Lemno-Spirodeletum (hydr.)	July 22–Aug. 19 1974	Mníšek village pond	SB
.3	Riccietum rhenanae (lit.)	June 1971	Nesyt	SM
•	Communities dominanted by l			~~~
.1	Bolboschoenetum maritimi continentale (lim.) B. maritimus ssp. compactus	July 26 1966	Kobylské jezero	SM
.2	+ Alisma plantago-aquatica Bolboschoenetum maritimi	July 26	Kobylské	SM
	continentale (lim.) B. maritimus ssp. compactus	1966	jezero	
.3	Glycerio fluitantis-Oenanthetum aquaticae-Bolboschoenus maritimus ssp. maritimus (lit.)	July 1972	Opato vický	SB
•	Communities of aerohydatoph	ytes (A.4, B.3)		
.1	Lemno-Utricularietum (limlit.) Utricularia vulgaris + Amblystegium riparium	June 1971	Nesyt	SM
.2	Batrachietum rionii (hydr.)	June 1971	Nesyt	SM
.3	B. rionii Batrachietum aquatilis (lit.) —peltatae	Aug. 15 1978	Žabka	\mathbf{SB}
.4	B. aquatile Hippuridetum vulgaris (lit.) H. vulgaris	June 1971	Nesyt	SM
•	Communities of eachydatophyt			_
.1	Elodeetum canadensis (hyd.) E. candensis	July 26 1963	Nový u Krče	SB
.2	Elodeetum canadensis (lit.) E. canadensis	July 1976	Malý Dubovec	SB

Table 2. (Cont.)

Biomass ² (kg . m ⁻²) aboveground underground	total	Sampling pattern ³	Author(s)
$\frac{1.50 - 2.22}{4.84 \pm 3 \times 0.17}$	6.34	$\frac{3-4\times0.5 \text{ m}^2}{\text{or } 4\times1 \text{ m}^2}$ $\frac{10\times0.5 \text{ m}^2}{10\times0.5 \text{ m}^2}$	Dykyjová et Hradecká (1976) Fiala (1976)
$\frac{1.75 - 3.00}{8.11 \pm 3 \times 0.41}$	9.86	$\frac{3-4\times0.5 \text{ m}^2}{\text{or } 4\times1 \text{ m}^2}$	Dykyjová et Hradecká (1976) Fiala (1976)
$\frac{1.83 \pm 3 \times 0.21}{5.24 \pm 3 \times 0.32}$	7.07	$\frac{10 \times 0.5 \text{ m}^2}{4 \times 1 \text{ m}^2}$ $\frac{20 \times 0.03 \text{ m}^2}{20 \times 0.03 \text{ m}^2}$	Květ, Svoboda et Fiala (1969)
$ \frac{0.24 \pm 3 \times 0.32}{0.87 \pm 3 \times 0.07} $ $ \frac{3.17 \pm 3 \times 0.52}{3.17 \pm 3 \times 0.52} $	4.04	$\frac{4 \times 1 \text{ m}^2}{10 \times 0.5 \text{ m}^2}$	FIALA et al. (1968) FIALA (1976) and Květ (1973)
	0.02 - 0.15 (29%)	Numerous samples of 0.1 m ²	Rejmánková (1973b)
	0.2 (14.5%)	Numerous samples of 0.1 m ²	Rejmánková (1979)
_	(14.5%) 0.01 (65%)	Numerous samples of 0.1 m ²	Rejmánková (1973b)
$\frac{0.78}{0.76}$	1.54	$\frac{8\times0.25~\mathrm{m^2}}{8\times0.04~\mathrm{m^2}}$	FIALA et KVĚT (1971)
$\frac{0.68}{1.11}$	1.79	$\frac{8\times0.25 \text{ m}^2}{8\times0.04 \text{ m}^2}$	FIALA et KVĚT (1971)
0.48		indirect sampling, along transect	Dykyjová et Ondok (1973)
	0.11 (cca 20%)	$4 \times 1 \text{ m}^2$	Rejmánková (1973b)
	0.11	$4 \times 1 \text{ m}^2$	Rejmánková (1973b)
	(25%) 0.09 (cca 15%)	$3 \times 0.5 \text{ m}^2$	J. Květ (in litt.)
	0.82 (26-28%)	$4 \times 1 \text{ m}^2$	Rejmánková (1973b)
	0.51 0.49 - 0.53	$3 \times 1 \text{ m}^2$	S. HEJNÝ et K. GREGOR (in litt.)
	(cca 17%) 0.47 (17%)	$6 \times 0.5 \text{ m}^2$	J. Рокоги́ et al. (in litt.)

Community type(s) (ecophase)		Date(s) ³	Locality	
+ de	ominant species		pond name	region
6.3	Potamogetonetum trichoidis (hydr.) P. trichoides, P. pusillus	June 29 1977	Kuvinský	SB
6. 4	Potamogetonetum trichoidis (lit.) P. pusillus	Aug. 15 1978	Žabka	\mathbf{SB}
6.5	Połamogetoneto-Zannichellietum pałustris (hydr.) Zannichellia pałustris	July 3 1963	Dubovec	SB
6.6	Potamogetoneto-Zannichellietum -pedicellatae (lithydr.) P. pectinatus, Z. palustris ssp. pedicellata	May 25 1971 June 1972	Výtopa & Nesyt	SM
7.	Communities of tenagophytes therophytes sensu Hejný 1960)	(B.2) (incl. pe	elochthophytes and	pelochto
7.1	Ranunculo scelerati-Rumicetum maritimi (terr.) R. sceleratus	July 24 1963	Korytný	SB
7.2	Polygono-Bidentetum tripartiti (lim.) B. tripartitus	July 19 1966	Kobylské jezero	SM
7.3	Initial stage of several community types (terr.) Polygonum lapathifolium Rumex maritimus, Alopecurus aeguali	August 1978	Žabka	SB
7.4	Eleocharitetum acicularis (lim.) E. acicularis	Aug. 24 1973	Přední Svinětický	\mathbf{SB}
7.5	Eleocharitetum acicularis (lim.) E. acicularis	Aug. 14 1974	Sádky u Třeboně	SB
7.6	Echinochloeto-Polygonetum ⁴ (terr.) Echinochloa crus-gali	July 28 1966	Kobylské jezero	SM

Table 2. (Cont.)

² Aboveground biomass only unless presented in the form of a fraction. An average ash content of 10% dry mass is assumed unless otherwise indicated (by the percentages given in parentheses). Ranges of some biomass values (or \pm three times their standard errors) indicate their spatial or temporal variation.

B. Unstable communities

B.1. Communities dominated by hydroochthophytes

These communities usually develop quite rapidly during a littoral-limosal ecoperiod on sites where the competitive abilities of the ochthohydrophytes and euhydatophytes or pleustophytes have been suppressed by a fall of water level. They become, however, most productive during the early stages of the subsequent limoso-littoral (to hydric) ecoperiod. They thus appear stenoecious in character. Phytocenologically, these communities mostly belong to the alliance *Bolboschoenion*

Biomass ² (kg . m ²) aboverground underground	total	Sampling pattern ³	Author(s)
	0.22	$5 \times 0.5 \text{ m}^2$	J. Роковиѓ et al. (in litt.
_	(17%) 0.10 (cca 15%)	$3 \times 0.5 \text{ m}^2$	J. Květ (in litt.)
_	0.63 0.54 - 0.73	$3 \times 1 \text{ m}^2$	S. HEJNÝ et K. GREGOR (in litt.)
_	(cca 15%) 0.12-0.17 (26.5%)	$8 \times 1 \text{ m}^2$	Rejmánková (1973b)
0.44 0.32 - 0.56	_	$3 \times 1 \text{ m}^2$	S. Hejný et K. Gregor (in litt.)
1.12	2.24	$8 \times 0.25 \text{ m}^2$	FIALA et KVĚT (1971)
1.12).46	0.88	$\frac{8 \times 0.04 \text{ m}^2}{6 \times 0.25 \text{ m}^2}$	J. Květ (in litt.)
0.40		$\frac{3\times0.125 \text{ m}^2}{3\times0.125 \text{ m}^2}$	
			Velásquez (1975)
0.42		$\overline{3 \times 0.125 \text{ m}^2}$	ζ, ,

³ Presentation in the form of a fraction indicates sampling date or pattern for aboveground biomass/that for underground biomass.

4 After HEJNÝ (1960).

maritimi DAHL et HADAČ 1941. They are typical of the smaller fishponds with short ecocycles. The existing data on their biomass, both above and below ground, are greatly variable: from several grams per 1 m² in the initial stages of community development to 0.5 to 1 kg . m⁻² of aboveground biomass only, in mature dense communities of monodominant Bolboschoenus maritimus or Oenanthe aquatica at limosal or a shallow littoral ecophase. Higher values are exceptional. This biomass fails to match that found in invasion stands of ochthohydrophytes for two reasons: one is the relatively shorter vegetation period of most hydroochthophytes, the other is their smaller permanent pool of underground biomass containing reserve substances. An exception are stands of Bolboschoenus maritimus in which the tubers

Comr	Community type	Net d.m. pro	Net d.m. production (kg.m ⁻² .year ⁻¹)	m ⁻² .year ⁻¹)	Net o.m.	Method of estimating
		above- ground	under- ground	total	production total (kg.m ⁻¹ .year ⁻¹)	net production
$1.1 \\ 1.2 \\ 1.3$	Caricetum gracilis Caricetum gracilis Caricetum gracilis	0.74 0.55 1.39	0.70 0.53 2.06	1.44 1.08 3.45	1.30 0.97 3.10	I. 1.15 $R_p/Sb = 1.1^*$ I. 1.16 $R_p/Sb = 1.1^*$ I. 1.16 $R_p/Sb = 1.7^*$
2.2	Schoenoplectetum lacustris Tumbatum Ichitolicae	2.03 1 55	2.12	4.15	3.74 1 86	I. 1.05 $R_p/Sb = 1.1$ I. 1.9 $P/Sb = 0.4$
2.5	1. gpheeum uurjoeae Typhetum angustifoliae T'umhetum ananstifoliae	1.67 2.05	1.10 1.42	2.67 3.47	2.40 3.13	$\sum_{\mathbf{R}_{\mathbf{D}}/\mathbf{S}\mathbf{b}} = \sum_{\mathbf{N}_{\mathbf{D}}/\mathbf{S}\mathbf{b}} = \sum_{\mathbf{N}_{\mathbf{D}}/\mathbf{S}\mathbf{b}} = \sum_{\mathbf{D}} \sum_{\mathbf{N}_{\mathbf{D}}/\mathbf{S}\mathbf{b}} = \sum_{\mathbf{D}} \sum$
2.6	Gyverietum my anna Gyverietum maximae Ghanietum manimus	0.90 - 1.57	0.28 - 0.48	1.18 - 2.05	1.06 - 1.85	$R_p/Sb = R_p/Sb = R$
- 80 C	Glycerietum maximae	1.29	0.40	1.69	1.52	$R_p/Sb = 1$
2.10	Sparganierum erecti Acoretum calami	0.83	$\begin{array}{c} 0.41 \\ 0.55 \\ 0.65 \end{array}$	1.81 1.38 2.2		1.1 $H_{p}/30 =$ 1.05 $H_{p}/Sb =$
2.12	Acoretum catamı Phragmitetum communis	$0.45 \\ 1.24$	0.30 0.83	0.75 2.07	0.66 1.86	1.05
2.13	Phragmitetum communis Phragmitetum communis	1.31 1.58 - 2.33	0.88 1.11 - 1.63	2.19 2.69 - 3.96	1.97 2.42—3.66	11 11
2.15	Phragmietum communis		1.29 - 2.21	3.13-5.36	2.82 - 4.82	$R_p/Sb =$
2.16 2.17	Phragmitetum communis Phragmitetum communis	$1.92 \\ 0.91$	$1.28 \\ 0.64$	$3.20 \\ 1.55$	2.88 1.40	I. 1.05 $R_p/Sb = 0.7$ I. 1.05 $R_p/Sb = 0.7$
$3.1 \\ 3.2$	Lemnetum gibbae Lemno-Spirodeletum	11	11	$0.30 \\ 0.43$	0.21 0.37	III. III.
4.1&2 4.3	4.1&2 Bolboschoenetum maritimi cont. 4.3 Glycerio fluitantis-Oenanthetum facies Bolboschoenus maritimus	$\begin{array}{c} 0.75 - 0.85 \\ 0.53 \end{array}$	1.02 - 1.17 0.72	1.77 - 2.02 1.25	1.59 - 1.82 1.13	$ \begin{array}{lll} I. \ I. I & R_p/Sb = 1.5 \\ I. \ I. I & R_p/Sb = 1.5 \\ \end{array} $
5.1 5.3 5.4	Lemno-Utricularietum Batrachietum rionii Batrachietum aquatilis Hippuridetum vudgaris			0.15 0.17 0.14 0.98	0.09 0.13 0.12 0.72	II. 1.4 II. 1.5 II. 1.5 II. 1.2

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II. 1.2 II. 1.2 II. 1.1 II. 1.1 II. 1.3 II. 1.3 II. 1.3	I. 1.1 $R_p/Sb = 1$ I. 1.1 $R_p/Sb = 1$ I. 1.1 $R_p/Sb = 1$ I. 1.05 $R_p/Sb = 0.6$
0.51 0.46 0.20 0.09 0.70 0.12-0.16	0.83 2.12 0.87 0.88
$\begin{array}{c} 0.61\\ 0.56\\ 0.24\\ 0.11\\ 0.82\\ 0.82\\ 0.16-0.22\end{array}$	0.92 2.35 0.97 0.98
1.1.1.1.1.1	0.44 1.12 0.46 0.40
	$\begin{array}{c} 0.48 \\ 1.23 \\ 0.51 \\ 0.58 \end{array}$
Elodeetum canadensis Elodeetum canadensis Potamogetonetum trichoidis Potamogetonetum trichoidis Potamogetoneto-Zannichellietum pedicellatae Potamogetoneto-Zannichellietum pedicellatae	Ranunculo scelerati-Rumicetum maritimi Polygono-Bidentetum tripartiti facios B. tripartitus Several initial stages Eleocharitetum acicularis
6.1 6.2 6.5 6.6 6.6	7.1 7.2 7.3 7.5

(Sb, listed in Table 2), the latter estimate being based on development of the undeground: aboveground biomass ratio in young polycormones. The resulting correction factors for shoot production and the R_p/Sb ratios used are indicated. I. After ONDOK et KVĚT (1978), KVĚT et HUSÁK (1978) and *SOUKUPOVÁ et al. (in litt.) by correcting for losses due to shoot mortality and leaf shedding, and by estimating the ratio of underground annual production (R_p) to seasonal peak shoot biomass

II. From an estimated turnover of biomass per year (based on phenological observations and data from the literature). The turnover factors used are indicated.

III. From seasonal changes in relative growth rate (REJMÁNKOVÁ 1979).

represent about 2/3 of the total biomass. High belowground production has been recorded in experimental cultures of this species: upto 1.9 kg \cdot m⁻². Estimates of an annual total net production of some 2.5 kg \cdot m⁻² thus do not seem unreasonable for fully developed dense stands of both *Bolboschoenus* subspecies (ssp. maritimus and ssp. compactus) that occur in fishponds, growing in nutrient-rich habitats at limosal ecophase. In view of its production-ecological characteristics as well as the survival of the tubers (they can remain alive dormant for several years, see HEJNÝ 1960), *Bolboschoenus maritimus* seems ecologically nearer to ochthohydrophytes than to the other typical hydroochthophytes such as *Sagittaria*, *Alisma* or *Oenanthe*.

B.2. Communities of tenagophytes

These communities are of short-term duration, hardly ever persisting on one site for more than two successive vegetation periods. The constituent species may be annual, biennial or perennial, shallow-rooted and with relatively short aerial shoots, as a rule. An optimum development of these communities is observed on emerging fishpond shores and bottoms during limoso-terrestrial ecoperiods. The limosal ecophase or a terrestrial ecophase with a very shallowly sunken water table bring about the highest net production in the tenagophyte communities if the soil fertility and weather conditions are favourable. Phytocenologically, the tenagophyte communities belong to several alliances. The seasonal peak total biomass rather closely approximates the total annual net production. Data are available on communities of the *Eleocharitetum acicularis* Koch 1926: over 0.6 kg. m⁻² for a nearly pure stand of *Eleocharis acicularis* at limosal ecophase in a pond, and 1.9 kg. m⁻² after fertilizer addition to a turf of *Eleocharis acicularis* kept experimentally at limosal ecophase (VELASQUEZ 1975). The high ash content in Eleocharis acicularis (22% on an average) has to be taken into account when considering these data. REJMÁNEK (1975) found a peak total biomass of about 0.6 kg. m⁻² in both an *Eleocharito* (ovatae)-Caricetum cyperoidis KLIKA 1935, facies with dominant Scirpus radicans, and a Bidenti-Polygonetum hydropiperis (W. KOCH 1926) LOHMEYER 1950, facies with dominant Alopecurus aequalis. These data seem illustrative of the production of therophyte communities in favourable habitats. In a Polygono-Bidentetum tripartiti (W. KOCH 1926) SISSINGH 1946, facies with Bidens tripartitus, FIALA et KVĚT (1971) found the net production to be markedly differentiated according to soil moisture supply in a clayey and nutrient-rich soil: from $0.4 \text{ g} \cdot \text{m}^{-2}$ in a dry situation on elevated ground to $2.2 \text{ kg} \cdot \text{m}^{-2}$ in a wet depression. Other biomass and production estimates made for tenagophyte communities, e.g., by Š. HUSÁK (in litteris) fall within this wide range. Great habitatinduced variation of production within individual community types seems more typical of the communities of tenagophytes than of any other communities occurring in fishponds: it is a feature of initial successional stages in general.

B.3. Communities of aerohydatophytes

Water-level fluctuations seem to promote the growth of certain aerohydatophytes and the production of their communities. A gradually falling water level particularly favours some batrachiids and myriophyllids, as exemplified by the data on a *Hippuridetum vulgaris* PASSARGE 1955 (REJMÁNKOVÁ 1973), occurring in a shallowly flooded fishpond bay, with the *Hippuris* shoots partly submerged and partly emerged: the total biomass amounted to about 0.8 kg. m⁻² and the estimated total annual net production did to some 1 kg. m⁻²; the average ash content was 15%. More data are, however, needed on the production of the unstable aerohydat ophyte communities formed by batrachiids and other plant growth-forms.

This brief survey is illustrated by the data characterizing the biomass and net primary production of macrophytes in particular stands of various communities, presented in Tables 2 and 3.

SUMMARY

The higher-plant (macrophyte) communities of the Central European fishponds are derived from the communities of the original wetlands and shallow waters. During the 4 to 6 centuries' history of the fishpond management, however, special types of the communities have developed. Their structure and functioning depend on the age of the pond, on the management category to which it belongs as well as on the intensity of the pond management. This has passed through three stages of which the recent one is characterized by the application of various measures greatly increasing the fish production and, at the same time, strongly affecting the fishpond vegetation and its habitats. With respect to the effects of the position of the water level and of its changes, the concept of the ecophases, ecoperiods and ecocycles is briefly reviewed. The stabilized (group A.) and unstable (group B.) higher plant communities are adapted, respecitvely, to a rather stable and fluctuating water level. Both groups of the communities comprise various life forms of aquatic and marsh plants. A survey of the available estimates of the biomass and net production of the higher plant communities occurring in the fishponds shows that these data are greatly diversified. The relatively stable communities dominated by the euryoecious species of the ochthohydrophytes are potentially the most productive. Others can produce large amounts of organic matter as well, provided their production processes are not limited by poor irradiance (which is the case in submerged communities or synusia), by lack of some mineral nutrient(s) (this may apply to all types of the communities) or by insufficient water supply (this applies to shallow-rooted tenagophytes in dry soil. to temporarily drying-out littoral reed or sedge marshes, etc.). The net primary production (or merely the biomass) of these plant communities thus becomes a sensitive indicator of the habitat.

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